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Particle Captures and the Method of Suspension Feeding by Echinoderm Larvae

MICHAEL W. HART

Department of Zoology, NJ-15, University of Washington, Seattle, Washington, 98195 and Friday Harbor Laboratories, 620 University Road, Friday Harbor, Washington, 98250

Abstract. Motivated by discrepancies between two recent descriptions of the suspension-feeding mechanism employed by echinoderm larvae, I describe particle captures by the larvae of seven species of temperate eastern Pacific echinoderms from four classes. When videotape recordings of free-swimming larvae clearing plastic spheres from suspension were analyzed, two modes of particle capture were observed to operate. The majority of captured spheres were caught at the peripheral ciliated band and then transported to the mouth, often by repeated capture on portions of the band progressively nearer to the mouth. This description is consistent with the ciliary reversal model of suspension feeding described by R. R. Strathmann. A small minority of captured spheres followed broad, curving paths directly into the larval mouth without interception at the ciliated band. These particle paths resemble those described by T. H. J. Gilmour. The videotape recordings also permitted a quantitative comparison of suspension feeding by these larvae. Several aspects of this behavior varied among developmental stages or among types of larvae, including: the distribution of particle captures among different segments of the ciliated band, the number of captures for single particles en route to the mouth, and the frequency of particles lost after initial capture. This variation raises a number of questions regarding the feeding performance of different larval species and the efficacy of these different larvae as elements of a reproductive strategy.

Introduction

The form and function of suspension-feeding aquatic animals is of wide interest, in part because they face a formidable challenge: concentrating materials and energy from a pool of resources that is both patchily distributed and highly dilute. Many different structures for concentrating food from suspension have evolved. These structures range from the relatively simple collar-cell filters of sponges to the morphologically and geometrically complex ciliated gills of bivalves and setose appendages of many crustaceans (Jørgensen, 1966). The method of capturing and concentrating food particles from suspension undoubtedly affects the effectiveness of particle capture and aspects of the growth and metabolism of suspension feeders (Conover, 1968). Inefficient suspension feeding may even limit the range of alternative strategies for growth and reproduction (McEdward and Strathmann, 1987). Thus, even if we were not generally curious about how organic particle filters work, there are particular reasons (the diversity of filters, and the physiological and evolutionary consequences of this diversity) for investigating the nature of different kinds of filters that remove food particles from suspension.

Suspension feeding by the planktonic larvae of echinoderms has been described by a number of authors (Gemmill, 1914, 1916; MacBride, 1914; Runnström, 1918; Meeks, 1927; Tattersall and Sheppard, 1934; Garstang, 1939; Strathmann, 1971, 1975; Strathmann *et al.*, 1972; Gilmour, 1985, 1986, 1988a, b). These larvae develop a band of tightly packed ciliated columnar epithelial cells (the ciliated band) that circumscribes the mouth, dividing the surface of the larva into circumoral and aboral fields (see Strathmann, 1971, 1975). Early workers offered divergent interpretations of the method by which these larvae concentrate suspended particles from seawater. They variously attributed larval feeding abilities to the actions of: (*i*) cilia on the circumoral field, (*ii*) water currents generated by the ciliated band, (*iii*) cilia surrounding

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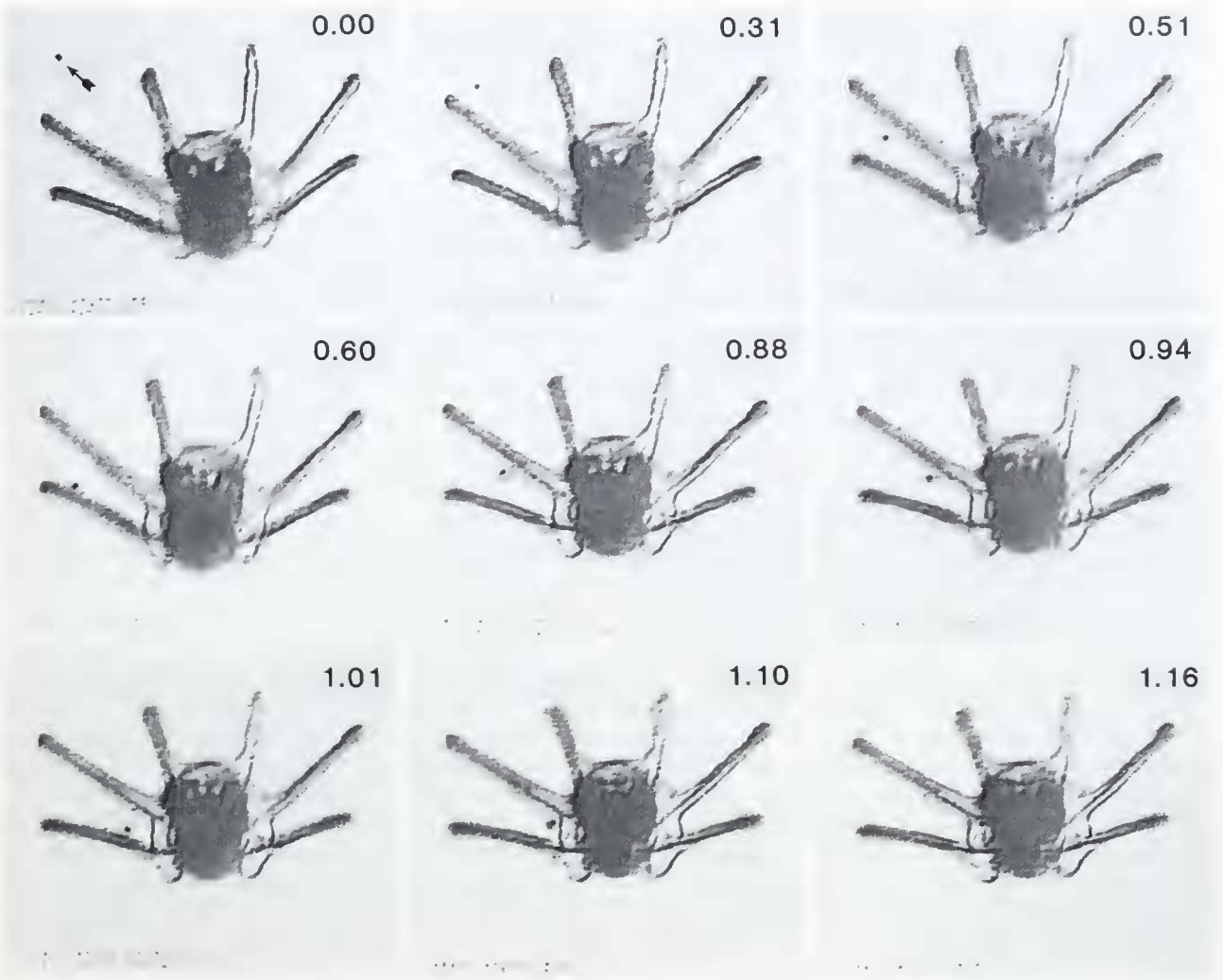

Figure 1. A collage of videotape frames showing the capture of a 20 μm diameter sphere by a six-armed echinopluteus (*Dendraster excentricus*). The number in the upper right of each panel is elapsed time in seconds (starting arbitrarily at 0 s). The arrow in the first panel shows the initial position of the particle. For scale, the arrow is about 135 μm long. The larva is shown in anterior ventral view, moving forward toward the top of each panel. The sphere moved toward the right postoral arm (0.00–0.51 s), was captured on the ciliated band and changed direction toward the base of the same arm (0.60–0.94 s), then was captured a second time near the base of the arm and moved toward the larval midline and mouth (1.01–1.16 s).

the mouth, and (*iv*) mucus secreted between opposed parts of the ciliated band. The more recent studies of Strathmann (1971) and Strathmann *et al.* (1972) resolved many of these conflicting descriptions: these studies suggest that echinoderm larvae remove particles from dilute suspensions by the brief reversal of the direction of the beat of cilia on the ciliated band. Particles are retained on the circumoral field, at the upstream side of the ciliated band, and then are transported toward the larval mouth. However, Gilmour (1985, 1986, 1988a, b) has disputed this interpretation of larval feeding and has suggested two completely different methods of particle capture.

Studies of suspension feeding by marine invertebrates often suffer from the inherent difficulty of relating rates of feeding to mechanisms of particle capture. For example, there is no general agreement on how the naplius larvae of copepods and barnacles capture particles, even though these are among the best-studied suspension feeders (reviewed by R. Strathmann, 1987). The feeding mechanism of nauplii is difficult to study because the movements of the feeding appendages and food particles are swift and complex. Measures of feeding rates of these animals are therefore restricted to indirect observations, such as the depletion of food particles (Paffenhöffer, 1971) or the in-

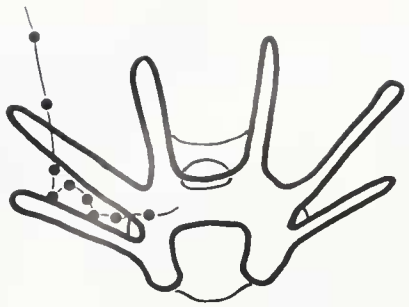

Figure 2. A cartoon of the particle capture sequence shown in Figure 1. The positions of the sphere in each panel of Figure 1 are indicated by the dots, and the particle path between these positions is interpolated by the solid line. The ciliated band of the larva is shown by the heavy lines; the mouth is shown in outline.

corporation of radioactivity from radiolabelled compounds in food particles (Marshall and Orr, 1956). However, without direct observations of feeding, it is difficult to relate variation in feeding rate (*e.g.*, among different naupliar stages) to variation in the morphological features (*e.g.*, the size and number of setae) that determine the feeding mechanism.

Unlike nauplii, the feeding larvae of echinoderms lend themselves to direct observation of particle capture. These larvae are relatively transparent, they swim with slow and continuous movement, and particle captures are sufficiently slow events that they can be counted and described with some precision. Given an accurate description of particle capture by these larvae, one can then interpret quantitative variation in feeding in terms of the particle capture mechanism. Echinoderm larvae are therefore excellent model organisms for comparative studies of form and function in suspension feeding.

In this report, I describe particle captures and suspension feeding by the larvae of seven species from four different echinoderm classes. A qualitative analysis of videotape recording (including still video images of particle captures) of free-swimming larvae clearing a dilute suspension of particles is generally consistent with Strathmann's description of the ciliary reversal suspension feeding mechanism. My observations also refute Gilmour's interpretation of the predominant method of particle capture by echinoderm larvae. However, a quantitative analysis of these recordings (which is difficult without a permanent record of larval behavior) leads to several novel inferences about larval feeding. First, these larvae appear to have two modes of particle capture: most particles are caught by apparent ciliary reversal at the ciliated band, but a small proportion of particles are captured without contacting the peripheral band, and this proportion does not vary among the different larvae examined. Second, changes in the distribution of particle captures on the ciliated bands of larvae do not correspond to changes in the lengths of particular segments of the band as larvae grow; some parts of the band appear to be more effective than others, and this discrepancy changes during larval development. Third, the number of independent ciliary reversals involved in a single particle capture (from the peripheral band to the mouth) varies among segments of the band, among developmental stages, and among species of echinoderms. These analyses also serve as a basis for quantitative comparisons of feeding performance among echinoderm larvae of different size, shape, and developmental stage that will be presented elsewhere.

Materials and Methods

Collection of adults

The sea urchin *Strongylocentrotus purpuratus* (Stimpson, 1857) (O. Echinoida) was collected from tidepools at Botanical Beach, Renfrew County, British Columbia, Canada. All other adults were collected from intertidal or shallow subtidal locations off the San Juan Islands, San Juan County, Washington, USA. *Strongylocentrotus droebachiensis* (O. F. Müller, 1776) and the sea star *Stylasterias forreri* (de Loriol, 1887) (O. Forcipulatida) were collected by dredge from San Juan Channel. The sea star *Dermasterias imbricata* (Grube, 1857) (O. Valvatida) was collected at 10 m depth from a rock wall off Turn Island. The sand dollar *Dendraster excentricus* (Eschscholtz, 1831) (O. Clypeasteroida) was collected from an intertidal bed in East Sound, Orcas Island. The brittle star *Ophiopholis aculeata* (L., 1767) (O. Ophiurida) was collected from a low intertidal cobble beach in Mitchell Bay on San Juan Island. The sea cucumber *Parastichopus californicus* (Stimpson, 1857) (O. Aspidochirotida) was collected at 15 m depth from a silt bottom off Brown Island.

Culture of embryos and larvae

Gametes, embryos, and larvae were treated according to methods described by M. Strathmann (1987). Gametes of echinoids were obtained by intracoelomic injection of 0.5 *M* KCl. Asteroid gonads were obtained by dissection; oocytes were induced to mature by incubation in 10^{-6} *M* 1-methyladenine in seawater. *Parastichopus* gonads were also obtained by dissection: oocytes were matured in a 1 $g \cdot l^{-1}$ solution of lyophilized radial nerve in seawater; and sperm were activated in 10 m*M* NH_4Cl in seawater. The radial nerves were obtained from the asteroid *Pycnopodia helianthoides* (Brandt, 1835). *Ophiopholis* females, in separate glass bowls filled with seawater, were allowed to warm on the benchtop for several hours and were thus induced to spawn; sperm were obtained by dissection.

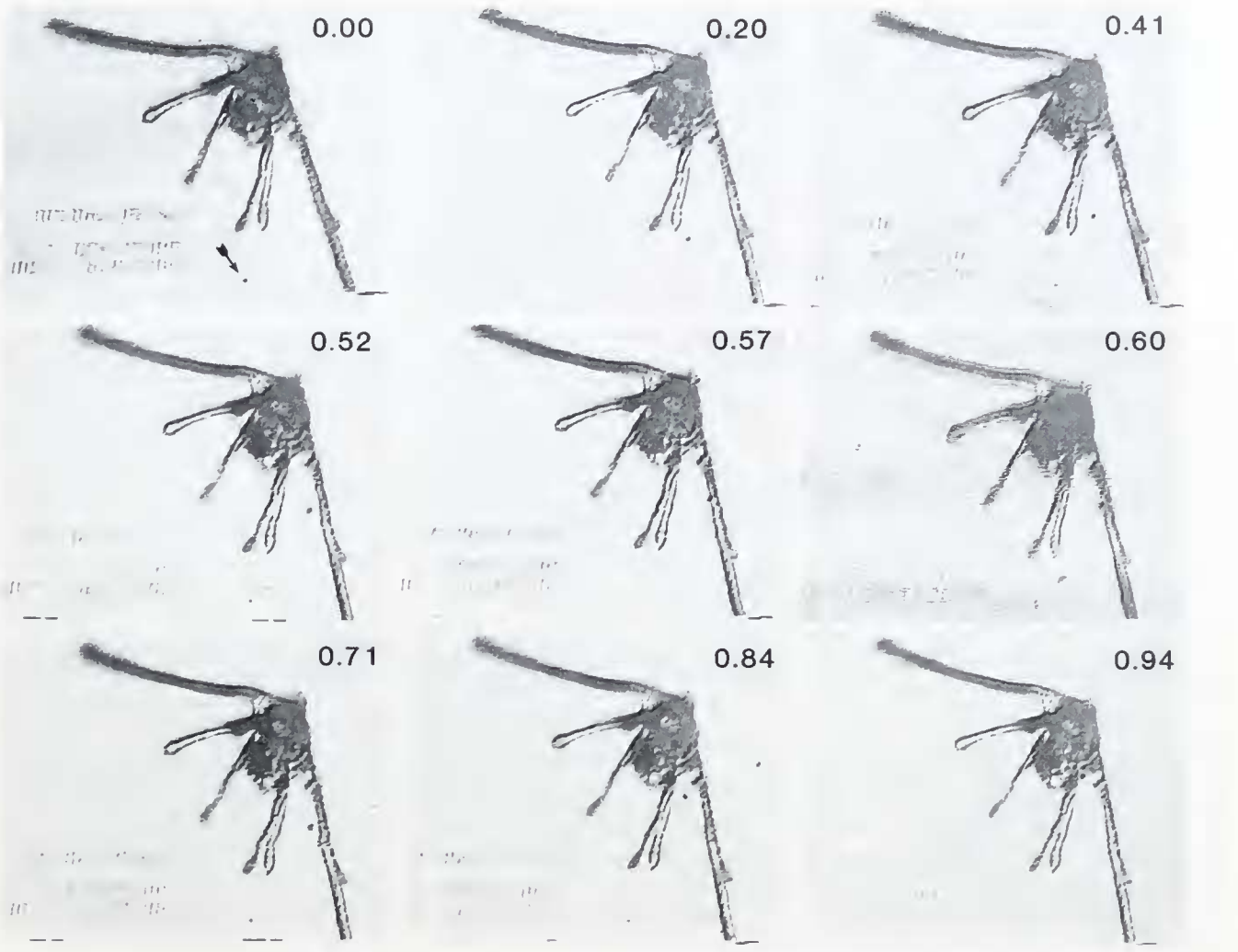

Figure 3. A collage of videotape frames showing the capture of a 20 μm diameter sphere by an eight-armed ophiopluteus (*Ophiopholis aculeata*) (the short postoral arms are not visible in this view). Numbers and arrow as in Figure 1. For scale, the arrow is 87 μm long. The larva is shown in anterior ventral view, moving forward toward the lower left of each panel. The sphere moved past the tips of the right anterolateral and posterodorsal arms (0.00–0.52 s), was captured on the right posterolateral arm (0.57–0.60 s), and changed direction back toward the larval mouth (0.71–0.94 s).

For all species, eggs were washed in 5-μm filtered seawater, fertilized with a few drops of a dilute sperm suspension, then washed again and transferred in groups of a few thousand to 3-l glass jars filled with filtered seawater. The jars were immersed in a flowing seawater bath at temperatures of 9–13°C (near local ambient sea temperature), stirred gently by paddles. Feeding larval stages were fed 2–3 ml per jar from dense cultures of each of three algae (*Dunaliella tertiolecta* Butcher, *Isochrysis galbana* Parke, and *Rhodomonas* sp.) at intervals of five to ten days coincident with water changes. These combinations of algae produced initial algal concentrations of about 10 cells μl^{-1} in the jars. Over five to ten days, groups of several hundred or thousand larvae, clearing 1–2 μl^{-1} min (averaged over time), probably captured most of this food.

Observing larval feeding

Larvae selected at random from the culture jar were placed singly, by pipette, into the bottom of a 63 ml cylindrical glass observation chamber (4.8 cm diameter by 3.5 cm deep) containing a suspension of 20 μm diameter polystyrene divinylbenzene microspheres (Duke Scientific) at a concentration of 2.4 μl^{-1} in filtered seawater. The concentration of spheres was reduced to 1 μl^{-1} for a few very large *Dermasterias* larvae with very high clearance rates. In those cases where the mouths of larvae were

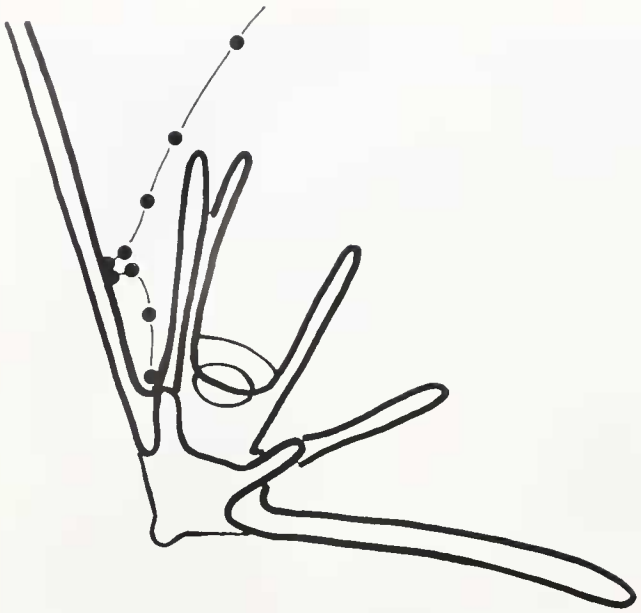

Figure 4. A cartoon of the particle capture sequence shown in Figure 3. The positions of the sphere in each panel of Figure 3 are indicated by the dots, and the particle path between these positions is interpolated by the solid line. The ciliated band of the larva is shown by the heavy lines; the mouth is shown in outline.

too small to ingest 20 μm spheres, or where small larvae were unable to capture these particles, 10 μm diameter spheres were used (these cases include all of the smaller *Ophiopholis* larvae, and several of the smallest *Dendraster, Parastichopus,* and *Strongylocentrotus purpuratus* larvae). The larger spheres were used whenever possible, because they were easier to identify and follow on videotape. Larvae of a wide range of sizes and developmental stages were used for all seven species. Temperatures inside the observation chamber could be held within 0.5–1.0°C of ambient seawater temperature because the chamber was equipped with a circulating seawater jacket. The top of the chamber was sealed with a clear plastic lid, eliminating trapped air and preventing image distortion by surface waves. As the larva swam from the bottom to the top of the chamber, several minutes of feeding were observed. For most larvae, several such feeding periods were observed. After each feeding period, the larva was returned to the bottom of the chamber by pipette and observed as it again swam upward.

Some larvae did not swim or capture spheres at high rates. These individuals were not used in subsequent analyses. Slow swimming, frequent stops, infrequent particle captures, or rejection of captured spheres by these larvae were probably the result of disturbance during transfer from the jar to the observation chamber. Under the conditions described, many larvae swam rapidly and had high clearance rates, but readers should not assume that larvae exhibit such behavior continuously, or that all larvae will do so under any conditions of observation.

I tried to get larvae to capture and ingest a number of other kinds of artificial particles, including Sephadex spheres of various sizes, other types of plastic spheres, and ragweed pollen, with variable success. I also used various unicellular algae. Some of these algae [*e.g., Isochrysis galbana, Pavlova lutheri* (Droop)] are small or non-refractile; others (e.g., *Dunaliella tertiolecta*) are larger but tend to clump in suspension. The most promising cultured unicellular organism was the dinoflagellate *Prorocentrum micans* Ehrenb., which is large and highly visible, does not clump, and keeps itself suspended in water by flagellar movements. Unfortunately, many larvae refused to capture or ingest these cells. Strathmann (1971) used the dinoflagellate *Amphidinium carteri* Hulburt, which I did not have in culture. Polystyrene spheres are useful for observations of suspension feeding because they are highly refractile, are available in a range of sizes, do not readily form clumps, settle from suspension slowly, and are readily captured and ingested by echinoderm larvae. An added advantage of indigestible particles is that larvae are unlikely to become quickly satiated as they clear particles from suspension.

Videotape recordings of larvae feeding were made with transmitted light at 30 frames s^{-1} with a videocamera mounted on the trinocular head of a dissecting microscope. I controlled both the focus and field of view manually. Thirteen to forty-four individuals were videotaped for each species, and I made some observations of feeding by larvae that were not taped. For illustrations of particle captures, single video frames were captured from the videotape by a frame grabber. The size and contrast of the sphere were increased in each of these images, and much of the background contrast was removed. These computer-enhanced images were then laser-printed and assembled into collages.

I calculated a clearance rate (volume of water cleared of particles per unit time, in μl min^{-1}) for each larva by counting particle captures and dividing the total number of captures by the length of the observation period, then dividing this capture rate (number min^{-1}) by the concentration of spheres in suspension (number μL^{-1}). Only periods of continuous swimming and feeding were used, therefore the calculated clearance rates represent maximum feeding performance over several minutes. A number of laboratory artifacts, including handling and transfer, high light intensity, and novel food particles, may affect the rate of feeding and the method of particle capture (Strathmann, 1971). Therefore, interpretations of the method of particle capture must be based on observations of larvae clearing particles from suspension at near maximal rates. High clearance rates indicate that the behavior of larvae in the laboratory has not been strongly altered by any of these

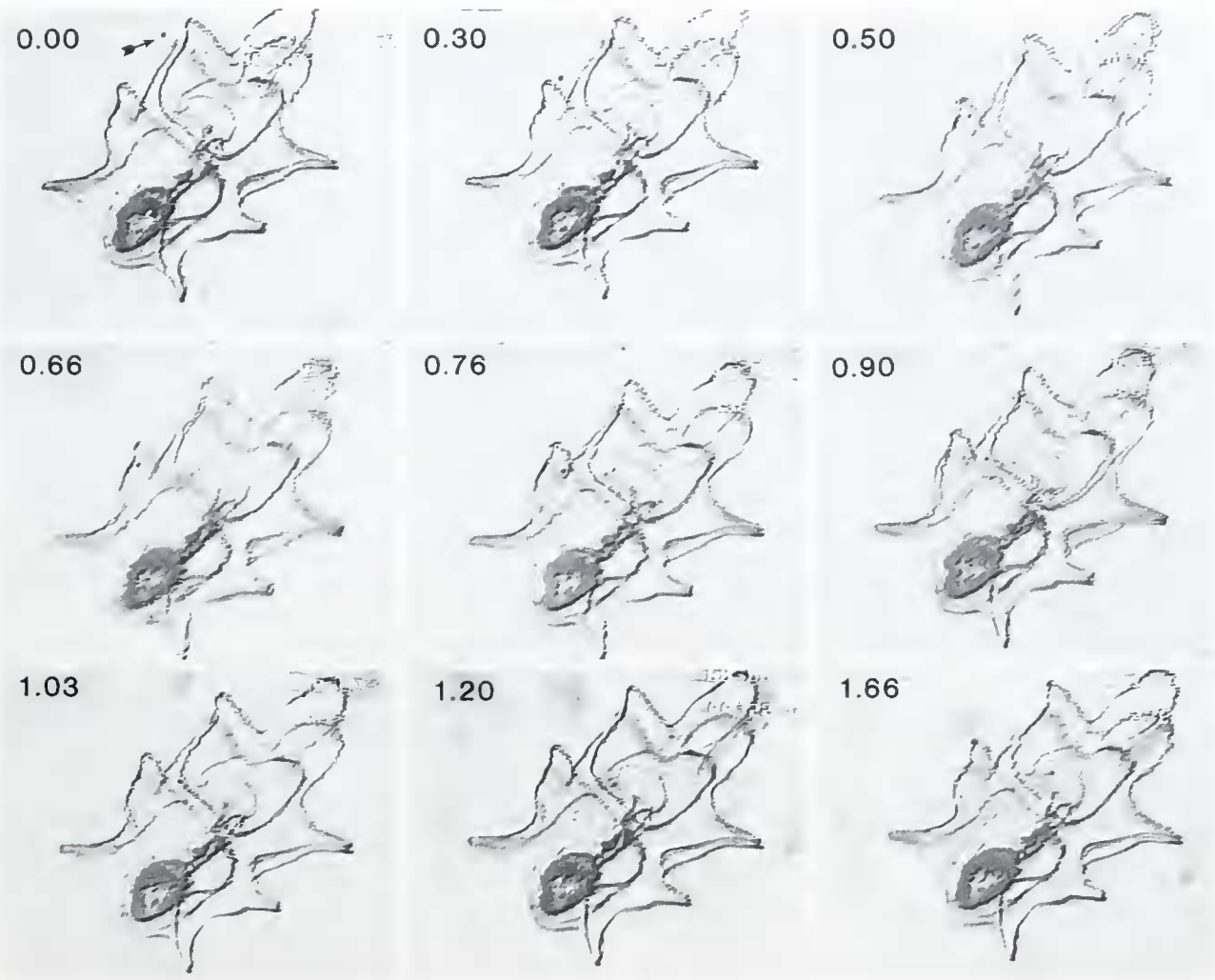

Figure 5. A collage of videotape frames showing the capture of a 20 μm diameter sphere by a bipinnaria (*Dermasterias imbricata*). Numbers (in the upper left) and arrow as in Figure 1. For scale, the arrow is 79 μm long. The larva is shown in ventral view, moving forward toward the upper right of each panel. The sphere approached the ciliated band on the right side lateral to the larval mouth (0.00–0.50 s), was captured there (0.66 s), and changed direction back toward the circumoral field (0.76–0.90 s). The sphere was captured a second time, on the preoral transverse ciliated band (1.03 s) and then swept into the mouth (1.20–1.66 s).

artifacts. Rates of growth and development of larvae in nature are probably often limited by low phytoplankton concentrations (Paulay *et al.*, 1985; but see Olson and Olson, 1989). High clearance rates are probably typical of larvae feeding on these dilute phytoplankton suspensions.

Measuring ciliated band lengths

Larvae were removed from the observation chamber, killed in a dilute solution of formalin in seawater, then mounted in a drop of seawater beneath a raised coverglass. Ciliated band length was estimated by summing the distances between sequential landmark points on the band (such as the tips and bases of the larval arms of plutei). The planar location of each landmark was determined by digitizing a camera lucida tracing of the band for each mounted larva; the location of each landmark in the third dimension, when in focus under the microscope, was determined from the vertical displacement of the microscope stage (McEdward, 1985).

Results

Particle captures

All larvae typically swam with the anterior end uppermost, from the bottom of the observation chamber, up

Figure 6. A cartoon of the particle capture sequence shown in Figure 5. The positions of the sphere in each panel of Figure 5 are indicated by the dots, and the particle path between these positions is interpolated by the solid line. The ciliated band of the larva is shown by the heavy lines; the mouth and stomach are shown in outline.

toward the observer and videocamera, capturing spheres as they swam. Runnström (1918) described this and a variety of other swimming postures; I observed some of them (most notably a lateral swimming direction, usually with the ventral side uppermost, as the larva swam slowly along the bottom of the chamber). These alternative swimming patterns were usually associated with low rates of feeding and frequent general ciliary arrests during which the larva came to a halt on the chamber bottom. I am not sure whether these behaviors are likely to be common in the plankton.

The aborally directed beat of cilia on the ciliated band produces water currents with a net posterior component that drives the larva forward while moving water laden with particles toward the ciliated band. Polystyrene spheres entrained in these currents approached the ciliated band on the upstream side of the band (usually on the arms of plutei, or on the loops of band between the bases of the arms, and on the anterior, posterior, and lateral portions of the band on bipinnariae and auriculariae). In cases where the proximity of the particle to the ciliated band could be judged, spheres appeared to approach within about one diameter of the surface of the larva (10–20 μm), less than the length of the cilia on most parts of the ciliated band (20–30 μm; Strathmann, 1971; McEdward, 1984). For larvae that were actively feeding, spheres approached the ciliated band, then abruptly changed direction at the band, and moved back toward the circumoral field rather than passing over the band toward the aboral field. On nearby portions of the band, water continued to pass over the band, while spheres were retained on the circumoral field (thus they were concentrated from suspension). Subsequent to this initial capture, spheres caught near the mouth often were swept immediately into the suboral pocket, probably aided by the beat of cilia on the circumoral field (Runnström, 1918) and by water currents generated by the aboral beat of cilia on the transverse portions of the ciliated band directly anterior and posterior to the mouth (the preoral and postoral transverse bands, respectively; see Strathmann, 1971). Spheres captured at any great distance (more than 50–100 μm) anterior or posterior to the mouth were often captured repeatedly on portions of the ciliated band progressively closer to the mouth; they were then transported to the mouth, probably by the same two mechanisms described above. I observed hundreds of such captures for each species examined; the specific descriptions that follow are for four particular species (one for each larval type), but they apply equivalently to other larvae of the same type.

Figures 1, 3, 5, and 7 show sequences of frames, from videotapes of particle captures like those described above, for an echinopluteus (*Dendraster excentricus*, Fig. 1), an ophiopluteus (*Ophiopholis aculeata*, Fig. 3), a bipinnaria (*Dermasterias imbricata*, Fig. 5), and an auricularia (*Parastichopus californicus*, Fig. 7). The accompanying line drawings (Figs. 2, 4, 6, and 8) depict the paths of spheres shown in the photocollages. These four pictorial accounts of particle captures are representative of almost all of the several thousand captures that I observed. Figures 1 and 2 show the abrupt change in direction of a sphere at the ciliated band of a six-armed echinopluteus, on the right postoral arm (the larva is shown in ventral view). The sphere was captured twice enroute to the mouth, once near the arm tip, and once nearer the base of the arm. A similar pluteus capture, on the right posterolateral arm of an advanced ophiopluteus, is shown in Figures 3 and 4. In this sequence, the sphere was held briefly on the ciliated band on the leading edge of the arm, then moved back toward the circumoral field (between the opposed bands on the arm) and the mouth. Because the oral hood above the mouths of these larvae is opaque, the end of the particle path cannot be followed into the mouth and esophagus. Figures 5 and 6 illustrate the capture of a sphere by a large bipinnaria: the sphere first approached the ciliated band on the right side of the larva, lateral to the suboral pocket and mouth. The sphere crossed the circumoral field, was arrested at the band, and moved back toward the mouth; it was captured again on the anterior transverse ciliated band (near the mouth) and was then swept into the mouth. A similar capture by an auricularia is shown in Figures 7 and 8; the sphere was captured first on the dorsal part of the ciliated band anterior

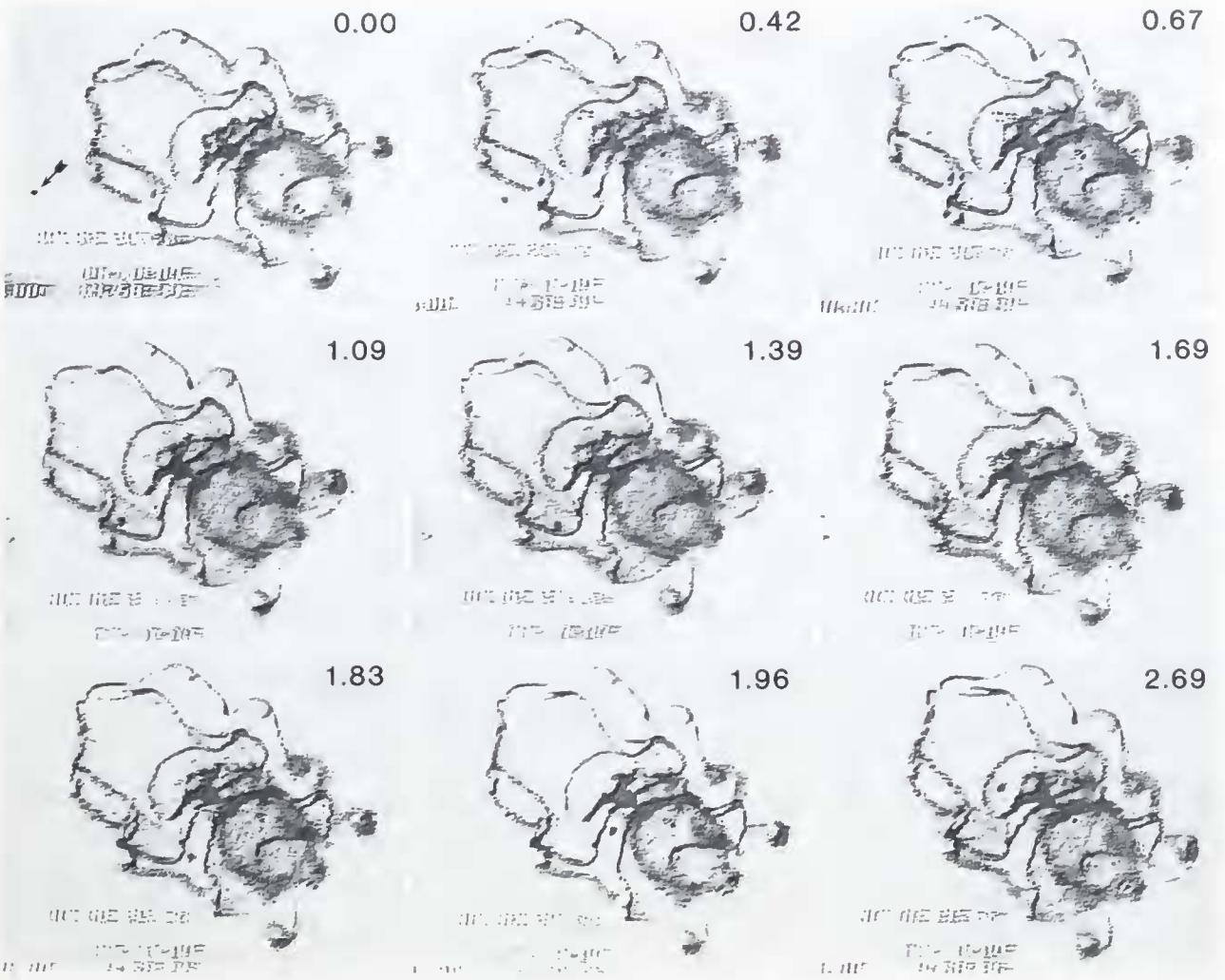

Figure 7. A collage of videotape frames showing the capture of a 20 μm diameter sphere by an auricularia (*Parastichopus californicus*). Numbers and arrow as in Figure 1. For scale, the arrow is 128 μm long. The larva is shown in ventral view, moving forward toward the upper left of each panel. The sphere approached the dorsal ciliated band on the right side anterior to the larval mouth (0.00–0.42 s), was captured there (0.067 s), and changed direction posteriorly along the circumoral field toward the right lateral portion of the band (1.09–1.39 s). The sphere was captured a second time, lateral to the mouth (1.69 s), and then moved toward the larval midline and into the mouth (1.83–2.69 s).

to the mouth, then was recaptured on the lateral ciliated band before entering the suboral pocket and mouth.

Larvae of all species occasionally captured spheres without close approach of the sphere to the ciliated band, and without abrupt change in the direction of movement of the sphere at the band. Such a particle capture (by the same *Dermasterias* larva illustrated in Figs. 5 and 6) is shown in Figures 9 and 10. These few spheres followed broad, curving paths into the suboral pocket of the larva, where they were swept into the larval mouth (probably by the current generated by the circumoral cilia). These particle paths resembled those described by Gilmour (1985, 1986, 1988b). Strathmann (1971) also depicted such particle captures, but did not emphasize their frequency or importance. I observed 44 individuals of *Strongylocentrotus droebachiensis* capture 1594 spheres; of these, only 80 (5.2%) were caught without an approach and a change of direction at the ciliated band. Similar proportions obtained for 13 *Parastichopus* (23 of 438 captures without ciliary reversals, (5.3%) and 17 *Dermasterias* (24 of 504 captures, 4.8%). These proportions do not vary significantly among species (compared by contingency table analysis, $\chi^2 = 0.118$, $P > 0.90$).

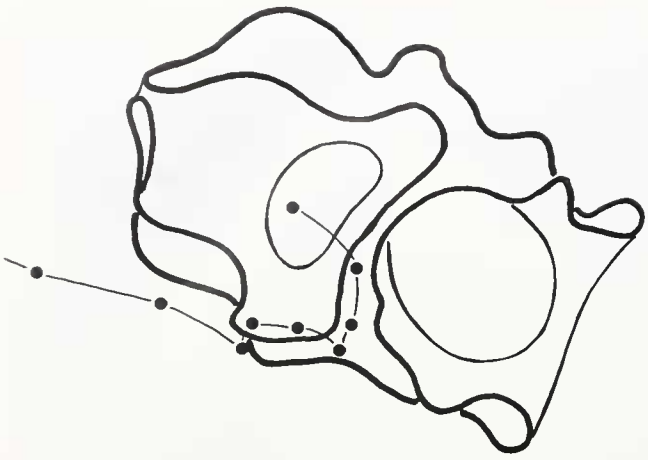

Figure 8. A cartoon of the particle capture sequence shown in Figure 7. The positions of the sphere in each panel of Figure 7 are indicated by the dots, and the particle path between these positions is interpolated by the solid line. The ciliated band of the larva is shown by the heavy lines; the mouth and stomach are shown in outline.

Some readers may be unconvinced that collages of still video frames can accurately represent the dynamic events involved in particle capture by these echinoderm larvae. I encourage such readers to photocopy the collages (enlarging them, if possible), to cut the frames of each collage out of the photocopy, and then to view the frames, as a stack of flip pictures, thus simulating the particle movement that occurs during the capture of spheres. Especially skeptical readers, who will be persuaded by nothing else, can contact me about receiving a copy of a short videotape sequence that demonstrates these particle captures.

The distribution of particle captures on ciliated bands

Spheres were caught on all parts of the ciliated bands of larvae, including the most anterior and posterior portions of the bands of auriculariae and bipinnariae and the tips of the arms of echinoplutei and ophioplutei. For *Parastichopus* larvae, 169 spheres (41.0%) were captured by ciliary reversal on the anterior portions of the ciliated band, 118 (28.5%) on the band lateral to the suboral pocket and mouth, and 127 (30.7%) on the portions of the band posterior to the mouth; for *Dermasterias* larvae, the same distribution was 242 (50.4%) anterior, 122 (25.4%) lateral, and 116 (24.2%) posterior captures (Table I). These distributions vary significantly between species (compared by contingency table analysis, $\chi^2 = 8.471$, $P = 0.015$), perhaps because the lengths of the different segments of the band vary as well. This is a difficult comparison (between the lengths of segments of the band and the proportion of captures by those segments) for bipinnariae and auriculariae, because the same landmarks that can be used to identify the locations of captures on videotape cannot always be precisely identified on the drawings of ciliated bands used to measure band lengths.

A similar comparison is more easily made among different developmental stages of echinoplutei, because such landmarks (the tips and bases of the larval arms) are readily identifiable on these larvae from all aspects. The growth of early pluteus stages involves the addition of ciliated band to only a few portions of the band (especially the postoral and anterolateral arms), whereas larger plutei grow by elongating other arm pairs, as well as that part of the band carried on the body of the larva (see Strathmann, 1971, 1975). All segments of the ciliated band (four arm pairs and the larval body) grew as *Strongylocentrotus droebachiensis* larvae progressed from four- to six- to eight-armed stages (Fig. 11); most of the *post hoc* pairwise contrasts (four- *vs.* six-armed, or six- *vs.* eight-armed) among these mean band lengths were significant (Table II). But in three cases, these size increases led to no measurable increase in the maximum clearance rate of the same segment (determined by counting particle captures on each segment). Eight-armed larvae had longer postoral and anterolateral arms, and longer ciliated bands on the larval body, than did six-armed larvae, but mean clearance rates for these segments of the ciliated band were no greater for the more advanced larval stage (Fig. 11, Table II). In a fourth case, feeding performance for one segment of the band declined: the length of the ciliated band borne on the larval body was similar for four-armed and six-armed stages, but the mean clearance rate for that portion of the band was significantly lower for the later larval stage. The lack of correspondence between size and performance of various parts of the ciliated bands of plutei suggests that some segments of the band are more effective at particle capture than other segments, and that this variation among segments changes as larvae develop.

Repeated capture of particles

One striking aspect of particle capture by echinoderm larvae was the repeated capture of individual spheres on the ciliated band. Figures 1 and 7 show good examples of such events. In many cases, these repeated captures produced a sort of pinball effect as spheres "bounced" from peripheral portions of the band to segments of the band nearer the mouth. I counted as many as 11 distinct capture events for single spheres caught by *Dermasterias* and *Parastichopus* larvae (Table I), though most spheres were captured 1–4 times, and even spheres captured near the most anterior or posterior ends of the band could be transported directly to the mouth after a single capture on the band. The mean number of captures varied among segments of the band (anterior, lateral, and posterior to

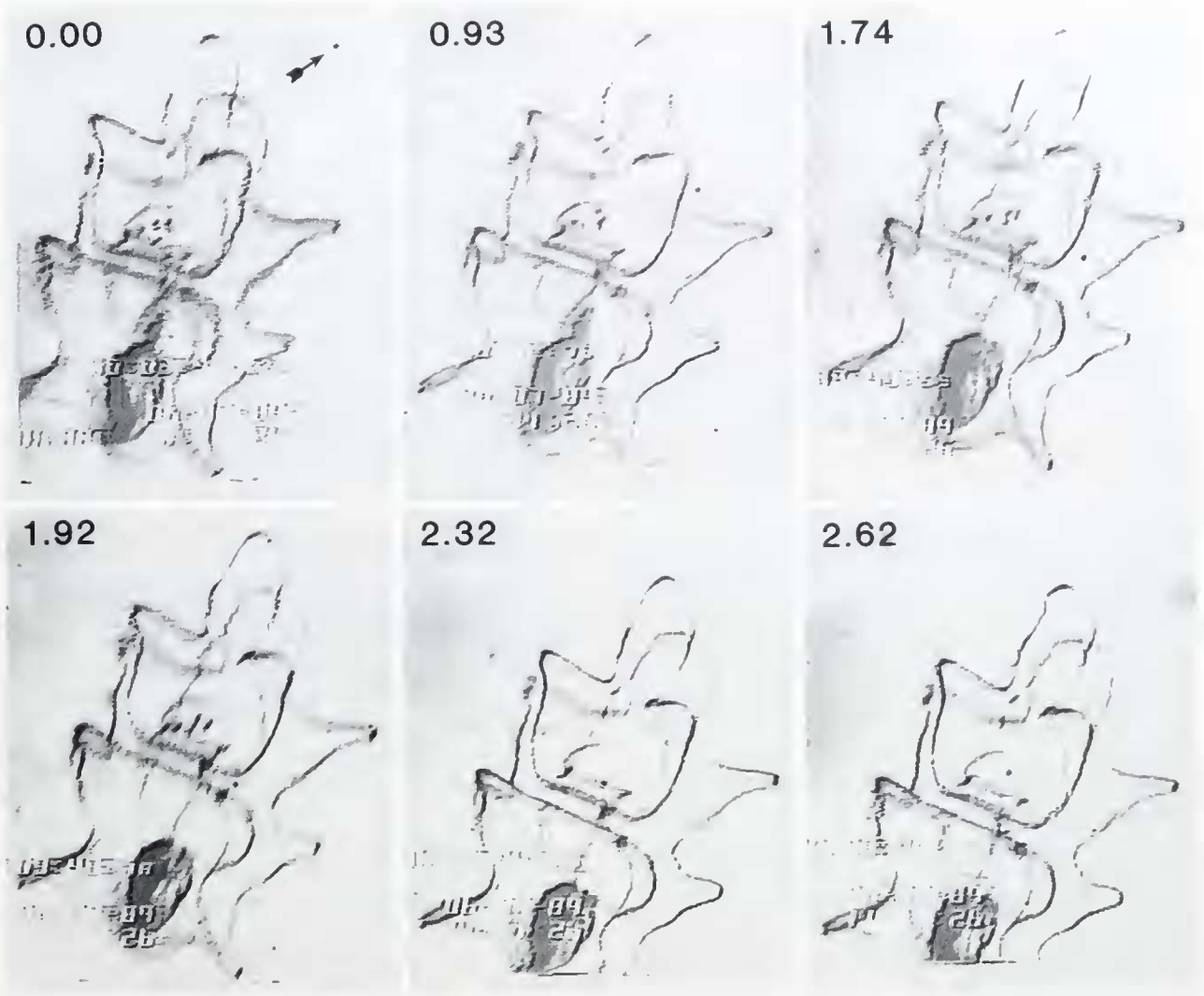

Figure 9. A collage of videotape frames showing the capture of a 20 μm diameter sphere by a bipinnaria (*Dermasterias imbricata*). Numbers and arrow as in Figure 5. For scale, the arrow is 89 μm long. The larva is shown in ventral view, moving forward toward the top of each panel. The sphere approached the left anterior side of the larva (0.00–1.74 s) and was swept directly into the larval mouth (1.92–2.62 s) without close approach to any part of the ciliated band and without changing direction at the band.

the mouth) for both species. Spheres initially caught lateral to the mouth were captured fewer times before ingestion than were spheres caught either anterior, or posterior, to the mouth (comparison of mean capture numbers by analysis of variance and *post hoc* contrasts for *Parastichopus,* $F = 39.60$; for *Dermasterias,* $F = 69.84$; for both comparisons, $P < 0.001$). Spheres caught initially on the anterior part of the ciliated band were also captured more times than those caught initially on the posterior end of the larva (for *Parastichopus,* $F = 16.96$, $P < 0.001$; for *Dermasterias,* $F = 5.60$; $P = 0.018$). The mean (± one standard deviation) number of captures for all spheres was also greater for *Parastichopus* (2.123 ± 1.254) than for *Dermasterias* (1.944 ± 0.890) (compared by *t*-test, $t = 2.488$, $P = 0.013$). These observations support the probable role of cilia on the circumoral field in transporting captured particles to the mouth. Spheres captured several hundred micrometers posterior to the mouth could be moved swiftly to the suboral pocket, in spite of the anterior direction of movement of the whole larva. In similar captures, larvae of *Parastichopus,* which lack circumoral ciliation (Strathmann, 1971), retained captured spheres more often en route to the mouth (see above) than did asteroid larvae, which have abundant circumoral cilia (Gemmill, 1914, 1916; Tattersall and Sheppard, 1934; Strathmann, 1971).

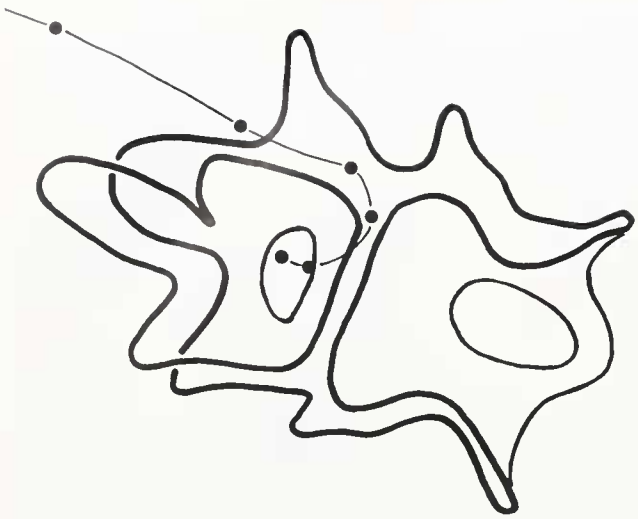

Figure 10. A cartoon of the particle capture sequence shown in Figure 9. The positions of the sphere in each panel of Figure 9 are indicated by the dots, and the particle path between these panels is interpolated by the solid line. The ciliated band of the larva is shown by the heavy lines; the mouth and stomach are shown in outline.

Most spheres caught by echinoplutei were captured just once on the ciliated band, but the incidence of multiple captures of spheres increased for *Strongylocentrotus drobachiensis* as these larvae developed more arms: for four-armed larvae (n = 9), 10.8 ± 2.7% (mean ± S.E.) of spheres captured were retained at more than one location on the ciliated band before entering the mouth; for six-armed larvae (n = 18), 16.1 ± 2.5%; for eight-armed larvae (n = 17), 21.6 ± 2.0%. Analysis of variance of arcsine-transformed proportions suggests that this is a significant increase in the incidence of multiple captures of spheres ($F = 4.11$, $P = 0.023$). Thus the complexity of particle paths to the mouth increases as plutei increase in size and change shape.

Retention of captured particles

Larvae of all species rarely failed to move to the mouth particles that had been removed from suspension at the ciliated band. For example, of 443 spheres captured by *Parastichopus* larvae at the ciliated band (where the site and number of captures for each sphere could be determined), only 29 (6.5%) were lost before reaching the mouth (Table I); *Dermasterias* larvae lost only 11 of 491 such spheres (2.2%). The frequency of loss did not vary significantly among segments of the band (anterior, lateral, and posterior to the mouth) for *Dermasterias* larvae (compared by contingency table analysis, $\chi^2 = 0.71$, $P > 0.25$). The same proportions varied significantly for *Parastichopus* ($\chi^2 = 12.33$, $P < 0.001$), mainly because I observed no spheres lost from the lateral portions of the ciliated bands of these larvae. The certainty of retention and transport from the initial site of capture to the mouth, often a distance of hundreds of micrometers, was remarkable. The exceptions to this generalization include a few small echinoplutei and bipinnariae that were unable to retain the larger spheres at the ciliated band, and some ophiuroid larvae that occasionally captured spheres without ingesting them. In these cases, some spheres approached the ciliated band on the upstream side, changed direction toward the circumoral field, then subsequently passes over the band and were lost. Thus, under some circumstances, some larvae may reject particles before they reach the mouth. Control over particle captures at the ciliated band may allow the collection of food to be inhibited even as the larva continues to swim forward

Table I

Mean number of captures for single spheres caught by larvae of (A) Parastichopus californicus *and (B)* Dermasterias imbricata

A. *Parastichopus californicus*

	Ciliated band segment		
	Anterior	Lateral	Posterior
	(Spheres ingested)		
$\bar{x}$ (range)	2.592 (1–11)	1.517 (1–7)	2.039 (1–5)
SD	1.510	0.855	0.858
n	169	118	127
	(Spheres not ingested)		
$\bar{x}$ (range)	2.643 (1–5)	—	2.733 (1–10)
SD	1.277	—	2.314
n	14	0	15

B. *Dermasterias imbricata*

	Ciliated band segment		
	Anterior	Lateral	Posterior
	(Spheres ingested)		
$\bar{x}$ (range)	2.211 (1–10)	1.369 (1–5)	1.991 (1–4)
SD	0.947	0.619	0.761
n	242	122	116
	(Spheres not ingested)		
$\bar{x}$ (range)	1.200 (1–2)	1.250 (1–2)	1.000 (1)
SD	0.447	0.500	0
n	5	4	2

Observations are tabulated by ciliated band segment (anterior, lateral, or posterior to the mouth of the larva) and by capture success (ingested or not ingested). SD = standard deviation; n = number of spheres.

under conditions where the mouth is jammed with particles, or the particles are not desirable, or the larva is attempting to reject particles from its buccal cavity (Strathmann, 1971).

Clearance rates

Maximum clearance rates ranged from 1–2 μl min^{-1} for early larval stages (four-armed plutei and the simple bipinnaria-shaped larvae of asteroids and holothuroids) with short ciliated bands, to 6–10 μl min^{-1} for late larval stages (the large eight-armed plutei and the bipinnariae and auriculariae with large loops and folds of the ciliated band) with longer bands. Maximum clearance rate increases with the length of the ciliated band in all of these larvae (Strathmann, 1971; M. Hart, unpub. data).

These clearance rates are similar to those of other larvae of comparable size and type, but measured by very different techniques. Strathmann (1971) measured clearance rates for larvae by two methods: counting algal cells entering the mouths of swimming larvae, or counting cells in the guts of larvae left briefly in algal suspensions. Lucas (1982) measured clearance rates for groups of larvae by estimating the depletion of algal cells from suspension in prolonged feeding trials (of about 24 h duration). The similar range of clearance rates estimated for larvae of similar types clearing algal cells or polystyrene spheres from suspension suggests that the use of artificial suspended particles can give accurate estimates of clearance rates. Flavoring particles with some transferable factor from algal cells may enhance the rate of ingestion of polystyrene spheres (Fenaux *et al.*, 1985), but larvae capturing unflavored spheres, in my study, ingested almost all of the spheres captured on the ciliated band (see below). Larvae may respond to particle flavor by altering the rate of forward swimming and water processing.

Although these different measuring techniques produce similar clearance rates, the techniques are not necessarily equivalent. Strathmann (1971) found that maximum clearance rates measured by counting algal cells captured

Table II

F-statistics and probability values for post hoc *paired comparisons of mean lengths and of mean maximum clearance rates among larval stages of* Strongylocentrotus droebachiensis, *for different segments of the ciliated band*

	Larval stage comparison	
Ciliated band segment	Four-armed (9) *vs* six-armed (18)	Six-armed *vs.* eight-armed (17)
Postoral arms		
length	F = 34.762***	F = 26.461***
maximum clearance rate	11.826***	3.030^{ns}
Anterolateral arms		
length	50.647***	38.756***
maximum clearance rate	12.149***	0.003^{ns}
Posterodorsal arms		
length	—	48.607***
maximum clearance rate	—	6.384*
Body		
length	0.954^{ns}	12.290***
maximum clearance rate	4.227*	1.617^{ns}

Note that only one set of comparisons for posterodorsal arms is made (four-armed larvae lack these arms). Numbers in parentheses indicate sample sizes for each larval stage. ***, $P \leq 0.001$; *, $P < 0.05$; ns, $P > 0.05$.

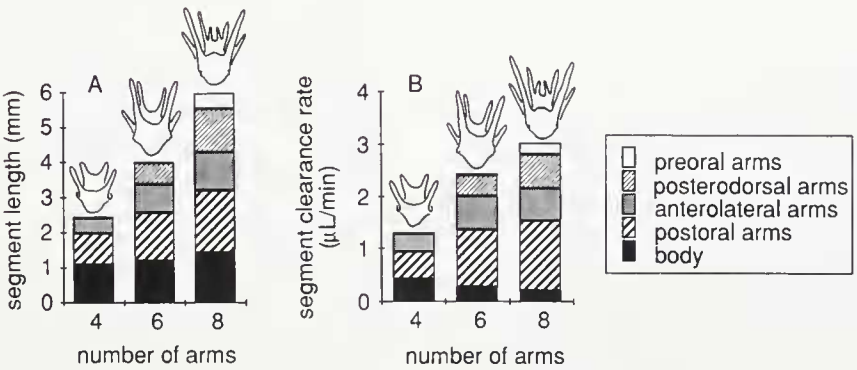

Figure 11. A bar graph showing the (A) length and (B) maximum clearance rate of different segments of the ciliated bands (borne on the larval body and on the postoral, anterolateral, posterodorsal, and preoral arms) for four-, six-, and eight-armed larvae of *Strongylocentrotus droebachiensis*. The total height of each bar indicates the mean ciliated band length or mean maximum clearance rate for whole larvae; for each bar, the height of segments with different shading indicates the same measures for particular segments of the ciliated band. Cartoons of larvae above each bar indicate the approximate changes in size and shape from one stage to the next.

during periods of 1–3 min were generally higher and less variable than those measured by counting algal cells in the guts of larvae left in algal suspensions for 5–13 min, presumably because the latter periods include some intervals when larvae are not feeding rapidly. Lucas' (1982) highest clearance rate for *Acanthaster* larvae (5.8 μl min^{-1} for early brachiolaria larvae) is much lower than the highest maximum rate that I measured for *Dermasterias* larvae of similar stage (10.0 μl min^{-1}). However, because of the large variance in clearance rates measured for different individuals, it is difficult to make precise contrasts among these three studies. Maximum clearance rates measured by watching larvae for a few minutes should usually be greater than rates measured by allowing larvae to feed for many minutes or hours, but other factors may obscure this effect.

One study is not consistent with the above prediction. Rivkin *et al.* (1986) found exceptionally high clearance rates (measured as the incorporation of radiolabel) for echinoderm larvae capturing [^{3}H]thymidine-labelled bacteria. For example, in feeding trials of ~4 h, the mean clearance rate for larvae of *Sterechinus neumayeri* (an echinoid) was 13.8 μl min^{-1}. The largest clearance rates (which were time-integrated *averages*) in their study must have been substantially higher: the mean + 1 SD clearance rate for *Sterechinus* was 18.5 μl min^{-1}. The largest *maximum* clearance rate I measured for an echinopluteus was 5.4 μl min^{-1} for a large *Dendraster excentricus*. This is a substantial difference. The thymidine-incorporation technique appears sound. Unless these Antarctic larvae are exceptionally large, these clearance rates may reflect a dramatic adaptation for the rapid capture of very small (<2 μm) particles. Measures of maximum clearance rates by direct observation of these larvae would be of considerable interest.

Ingestion of particles

Most larvae ingested captured spheres by accumulating a bolus of spheres in the middle and lower esophagus. They then swallowed the bolus into the stomach by a rapid peristaltic contraction accompanied by opening of the cardiac sphincter. Most other workers have observed the same process. Other individuals, at times, did not readily ingest spheres, but instead accumulated them in a whirling mass that rotated within the buccal cavity under the influence of water currents directed into the mouth by the adoral cilia, and out of the suboral pocket by the transverse ciliated bands. If this mass of spheres was not ingested, it was eventually rejected from the buccal cavity, probably by reversal of the direction of beat of the adoral or other cilia of the buccal cavity (MacBride, 1914; Gemmill, 1914, 1916; Runnström, 1918; Strathmann, 1971), and then moved out of the suboral pocket over the postoral transverse band. Rejection of a mass of spheres was not accompanied by a general arrest or reversal of beat of the cilia on the ciliated band (*i.e.*, the larvae did not stop swimming or swim backward), and the rejected mass was not captured again at the postoral transverse band. These events indicate an impressive subtlety of control over ciliary beat that is probably modulated by the larval nervous system (Burke, 1978, 1983).

Discussion

Methods of suspension feeding by echinoderm larvae

My observations of particle capture by echinoderm larvae suggest a resolution of the conflicting accounts of suspension feeding by these larvae. The majority of particle captures (by all of the stages and species of larvae that I examined) were similar to those described by Strathmann (1971). The retention of particles on the upstream side of the ciliated band of larvae, accompanied by a change in the direction of particle movement toward the circumoral field, supports the hypothesis that echinoderm larvae remove particles from suspension mainly by a brief, localized reversal in the direction of beat of cilia on the ciliated band (Strathmann *et al.*, 1972). However, about 5% of all particle captures appeared to occur without the close approach of the particle to the ciliated band and without an abrupt change in the direction of particle movement at the band. This proportion was similar among the three species I examined; larvae of a fourth species (*Stylasterias forreri*) also captured about 5% of the particles that they encountered when prevented from generating ciliary reversals (Hart, 1990). The paths of particles caught by this second method were reminiscent of those described by Gilmour (1985, 1986, 1988b) for echinoplutei and bipinnariae.

The resolution of these conflicting descriptions depends on two factors: the availability of videotape as a permanent record of behavior suitable for quantitative analysis; and high rates of partical clearance, indicating normal larval behavior uncompromised by laboratory artifacts. Lacking any permanent record of larval feeding, Strathmann probably described only the most common mode of particle capture that he observed for free-swimming larvae in relatively large volumes of seawater. For his part, Gilmour has principally described particle captures by larvae attached to suction pipettes or trapped between glass surfaces, and such methods of manipulating and orienting larvae for observation may disrupt normal swimming and feeding behaviors, due to the disturbing effects of strong suction by the pipette, or to the close proximity of surfaces and their large effect on flow patterns at low Reynolds numbers (Vogel, 1981). Larvae may respond to these dis-

turbances with reduced clearance rates. At low clearance rates, a few particles may enter the mouths of echinoderm larvae without apparent change of direction at the ciliated band, but this is not the method of particle capture that is most common when larvae are processing water at high rates (Strathmann, 1971, 1982; Hart, 1990). The particle paths described by Gilmour (1985) also occur in free-swimming larvae, but at a lower frequency than his studies suggest. Because he has not reported clearance rates in any of his studies, it is difficult to interpret Gilmour's observations. Gilmour has probably observed larvae that are not actively feeding. To the extent that larvae exhibit such behavior in nature (perhaps in dense phytoplankton patches, or in response to other disturbances), these observations may indicate the lower limit of the capacity of larvae to reduce clearance rate in situations where feeding is actively suppressed. Gilmour's methods are useful for some kinds of observations, and larvae may feed at high rates under these conditions if care is taken, but the interpretation of observations on methods of suspension feeding made under such conditions also requires careful consideration.

I cannot account for the differences between Gilmour's (1988a) description of particle capture by the auricularia of *Parastichopus californicus* and my own observations of feeding by these larvae. *Parastichopus* larvae in my study removed large numbers of spheres from suspension in a manner identical with that of plutei and bipinnariae. I could not confirm Gilmour's (1988a) observation that an encounter between an auricularia and a particle results in a brief reversal in the direction of rotation of the larva and entry of the particle to the suboral pocket. The rotation of these larvae was not disturbed by particle capture, and they cleared spheres from suspension at rates comparable to those for other larvae of similar size and developmental stage.

The kinds of descriptions I have presented are crucial for the interpretation of quantitative aspects of suspension feeding. For example, the observation that echinoderm larvae retain captured particles at the ciliated band leads to the prediction that the clearance rates of these larvae should increase as their ciliated bands grow longer during development (Strathmann, 1971). Such explicit predictions are more difficult to derive for larvae (or other suspension feeders) where feeding rates cannot be determined by direct observation. For echinoderm larvae, one can now try to interpret ontogenetic and phylogenetic variation in feeding rates as a consequence of the variation in the length and arrangement of the ciliated band (see below).

Larval shapes and the development of ciliated bands

The forms of echinoderm larvae vary among classes, among species within classes, and among developmental stages of single species. Suspension feeding by these larvae covaries in several ways with these form differences. For example, the number of capture events for single particles varied among parts of the ciliated bands of both bipinnariae and auriculariae, and the same measure (averaged over all segments) varied between these two larval forms. The most significant of these differences, I think, are the distribution of particle captures among segments of the ciliated bands of echinoplutei and the change in this distribution during larval development. For *Strongylocentrotus droebachiensis*, the clearance rate of a single segment of the band was not necessarily reflected in the growth of that segment as the larva grows and adds new larval arms. The surprising implication of this result is that some ciliated bands (on a single larva) are more effective suspension-feeding devices than are other bands. LaBarbera (1981) made a similar observation for adult articulate brachiopods. The ciliated lophophore of these animals consists of a pair of lateral arms and a median coil. The area-specific pumping rate (which would be proportional to a clearance rate if LaBarbera had observed particle captures instead of dye stream movement) of the median coil was only about 60% of the rate for the lateral arms. LaBarbera ascribed this difference to the geometrical arrangement of the different parts of the lophophore and the consequences of this geometry for shear stress and viscous energy loss (resulting in lower fluid flow rates) over the median coil.

This inference (of shape effects on feeding performance) could clearly be extended to variations on the pluteus form among echinoid species, or to variation among the basic larval forms of different echinoderm classes. Emlet (1991) has predicted that such effects could arise from ontogenetic changes in larval shape or from phylogenetic variation in ciliated band arrangement. Using scaled models of whole larvae with different shapes, or of isolated ciliated bands with different orientation, Emlet showed that changes in both the gross morphology of larvae and the arrangement of ciliated bands could enhance particle capture rates (by increasing velocity gradients and fluid flow rates over the band). My direct measurements of the feeding performance of different ciliated bands confirm that performance differences among larvae of different development stages do manifest themselves, possibly due to the fluid-mechanical effects described by Emlet. Other observations (M. Hart, unpub. data) suggest that these effects may also extend to comparisons among different types of echinoderm larvae. If the geometrical development of a ciliated band affects the functional performance of that band, then there may be taxonomic biases in performance associated with evolutionarily conserved differences in patterns of larval development.

The evolution of larval form and reproductive strategies

Two general conclusions derive from the previous discussion: all feeding echinoderm larvae employ the same mechanisms to concentrate food particles from suspension; and quantitative aspects of feeding by these larvae change during larval development. These conclusions invite some interesting corollaries. First, the method of particle capture by echinoderm larvae has remained similar among different classes in spite of considerable evolution of larval form. The four types of echinoderm larvae are not necessarily related phylogenetically in a manner obvious from their gross organization. Raff *et al.* (1988), Smiley (1988), Smith (1988), and Strathmann (1988) have all recently proposed phylogenies for the extant echinoderm classes based on different combinations of morphological, embryological, and molecular information. In spite of the apparent similarities in elaboration and organization of the ciliated band between ophiuroid and echinoid larvae, and between holothuroid and asteroid larvae, few of these phylogenies group the pairs of classes together in this way. There are relatively few points of agreement among the different phylogenies or among their authors. One is left to conclude that there may have been both convergent and divergent evolution of larval form in echinoderms. However, the method of suspension feeding by echinoderm larvae has apparently been strongly conserved throughout the evolutionary history of the phylum (though numerous groups have lost the means and requirement to feed during larval development).

Second, quantitative variation in feeding among echinoderm larvae may imply variation in the effectiveness of these different larvae as elements of a reproductive strategy. Echinoderm larvae (and other feeding larval forms) can be thought of as devices for turning small eggs into large juveniles (by concentrating materials and energy from the plankton). The effectiveness of these devices turns on the relative rates of development and mortality during larval life. The availability of food to larvae affects the development of larval and juvenile structures and the duration of the larval period (Fenaux *et al.*, 1985; Paulay *et al.*, 1985; Hart and Scheibling, 1988). Larval duration figures prominently in several theoretical and comparative treatments of life history evolution in marine invertebrates (Vance, 1973; Christiansen and Fenchel, 1979; Strathmann, 1985; Emlet *et al.*, 1987). Although all of the larvae that I have observed use the same methods to remove particles from suspension, they vary considerably in the organization and development of the ciliated band (see Figs. 2, 4, 6, 8). Some quantitative aspects of larval feeding vary as larvae change shape, or vary among larvae of different classes. This variation may be reflected in measures of clearance rates for different larvae. In this case, we could reject the tacit assumption that all larvae are equivalent solutions to the problem of building a large juvenile from a small egg. The functional and life-historical consequences of such a result are the subject of a second paper.

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